

REDESCRIPTION AND ANATOMY OF THE VIVIPAROUS FRESHWATER
GASTROPOD *HEMISINUS LINEOLATUS* (W. WOOD, 1828)
FROM JAMAICA (CERITHIOIDEA, THIARIDAE)

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ABSTRACT

The West Indies, well known for its distinctive geological history, is well suited for studies in biogeography and biodiversity. However, the lack of comprehensive studies for much of its unique fauna has hampered insights into their systematics, evolution and phylogeography. The scarcity of data is particularly pronounced for freshwater gastropods in the viviparous family Thiaridae – represented in the archipelago by *Hemisinus* Swainson, 1840 and *Cubaedomus* Morrison, 1951. Hitherto described only on the basis of shell morphology, we here redescribe *Hemisinus lineolatus* (W. Wood, 1828), the type species of *Hemisinus*, based on type material and museum collections. The anatomy of this species is also described, representing the first such comprehensive study of any Neotropical thiarid. The synonymy of *Hemisinus buccinoides* Reeve, 1860, with *H. lineolatus* is confirmed. The species is found to possess a mixture of distinctly thiarid features (e.g., operculum, rachidian, midgut, brood pouch) and features previously undocumented in the family (e.g., gonochorism with ~equal sex ratios, glandular pallial oviduct with spermatophore bursa in lateral lamina, spermatophore organ, statoconia). Some of these features (e.g., statoconia, spermatophore organ) are also found in members of the apparent sister group to the Thiaridae – the African-Asian freshwater Paludomidae. Consequently, the combination of features in *Hemisinus* is consistent with a basal position in the family.

Key words: morphology, systematics, Paludomidae, brood pouch, Greater Antilles, Neotropics.

INTRODUCTION

Located within the Caribbean Plate, the islands of the West Indies have been considered a laboratory of biogeography and evolution (Ricklefs & Bermingham, 2008). The West Indian islands are sufficiently isolated to favor the presence of endemism in many groups of organisms, but they are also close enough to each other and to the mainland to allow a dynamic interaction with the surrounding continents (Buskirk, 1985; Woods, 1989; Iturralde-Vinent & MacPhee, 1999; Hedges, 2001, 2006; Woods & Sergile, 2001). The West Indian archipelago is composed of three groups of islands: the Greater Antilles, the Bahamas, and the Lesser Antilles. Jamaica, the third largest island of the Greater Antilles, is considered to be one Caribbean biogeographical

region by itself, as result of its unique geology and faunal endemism (Bland, 1866; Buskirk, 1985; Iturralde-Vinent & MacPhee, 1999). On Jamaica, while the land snail fauna appears to be the most varied and unique among the whole West Indies archipelago (Bland, 1866; Goodfriend, 1986; Paul & Donovan, 2005; Rosenberg & Muratov, 2006), it seems to be the opposite for the freshwater representatives; the freshwater mollusks mainly belong to cosmopolitan genera, with exceptions only among the ampullariids (Ampullarioidea) and thiarids (Cerithioidea) (Simpson, 1894; Russell-Hunter, 1955).

Although freshwater cerithioideans are one of the richest gastropod components of freshwater faunas in the tropical areas of the world (Strong et al., 2008), they are still relatively poorly studied in the Neotropics. The generic

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names *Aylacostoma* Spix, 1827, *Hemisinus* Swainson, 1840, and *Cubaedomus* Morrison, 1951, together with the subgenera *Semisinus* Morelet, 1849, *Verena* Moricand, 1841, *Longiverena* Spix, 1827, and *Basistoma* Lea, 1852, have been assigned to taxa inhabiting Central and/or South America (Chenu, 1859; Fischer, 1885; Thiele, 1928; Pilsbry & Olsson, 1935; Morrison, 1951, 1954; Jaeckel, 1969; Nuttall, 1990). Among these taxa, the limits between them still remain to be established. As a consequence, the distributional range for such genera as *Hemisinus*, which was originally allocated to Jamaica and Cuba, progressively expanded since the mid 19th century to include Central America, Peru, Venezuela, Surinam, Brazil and the Paraguay River (Reeve, 1860; Brot, 1862; Martens, 1873; Fischer, 1885; Ihering, 1901, 1909; Vernhout, 1914; Hylton-Scott, 1954; Simone, 2006). The same applies to those fossil shells that have been assigned to the Thiaridae due to superficial resemblance (e.g. Nuttall, 1990).

Knowledge of the Jamaican Thiaridae, based solely on 19th century shell descriptions made by such naturalists as Adams (1845, 1849, 1851), Chitty (1853), Bland (1861, 1866), and Vendryes (1899), has hardly increased since. Unfortunately, these studies failed to record precise localities. From Jamaica, *Hemisinus lineolatus* (W. Wood, 1828) and *H. buccinoides* Reeve, 1860, have been described based on the morphology of single or few shells. In order to shed light on the history of the genus *Hemisinus*, this paper aims to use geographic data, in an integrative approach, on occurrences, shell morphology and the soft body anatomy to resolve the taxonomy and systematics of these enigmatic natives of the West Indies.

MATERIALS AND METHODS

The reviewed collections are composed mainly of specimens obtained on Jamaica's easily accessible areas, such as Montego Bay or Bog Walk, whereas the eastern territories have been poorly sampled (Fig. 2). Embryonic shells were measured from scanning electron micrographs. Adult shells were measured with calipers with a precision of 0.1 mm ($n = 874$). Measurements include shell height and width, aperture length and width, length of the last whorl, length of the last three whorls, and whorl number. After exploratory statistical analysis (data not shown), 44 juvenile shells were ex-

cluded from subsequent analyses to diminish the number of outliers. In order to compare type material for the two Jamaican nominal taxa to each other and to other Antillean samples, multivariate and graphical statistic analyses were performed. Because the variables mentioned above are in different units, all variables were normalized by dividing the raw values by their standard deviations (data not shown). A Principal Components Analysis (PCA) was performed using Palaeontological Statistics version 1.68 (Hammer et al., 2001). The two most explanatory variables identified via PCA, were compared graphically (scatterplot, boxplot) in SPSS 15.0 for Windows.

Samples preserved in 70% ethanol were used for anatomy, histology, radulae extraction, and SEM observation of embryonic shells. Remarkable is the scarcity of sufficient and adequately preserved soft body samples. The anatomical studies here presented are based on the examination of 30 female and male specimens of *H. lineolatus* from the ANSP and ZMB collections. The anatomy was studied using a Leica stereo microscope MZ 9.5 with camera lucida. Midgut anatomy is based on three specimens (ANSP 12088A, $n = 1$; ANSP 12087I, $n = 2$), and was studied by cutting around the periphery of the midgut chamber along the posterior, right and anterior margins and deflecting the roof to the left. Complete male and female bodies, as well as isolated male and female pallial gonoducts, were studied histologically (ANSP 12087I, $n = 4$). Two females (ANSP 12087H) containing embryonic shells in the brood pouch were decalcified in successive solutions of 7% nitric acid (HNO_3 ; for three days), sodium sulphate (Na_2SO_4 ; for one day) and distilled water (one day) according to Romeis (1989). Specimens were dehydrated and paraffin embedded using an automatic Shandon Hypercenter XP 167506S. Tissues were sectioned at 12 μm on a Leica SM 2000R microtome, stained with haematoxylin/eosin and preserved with Canada balsam. Histological serial sections were photographed with a microscanning Jenoptik Prog/Res 3012.

The radula was extracted and cleaned as described by Holznagel (1998). Cusp/denticle formula is as follows: (1) rachidian (number of left side cusps/median denticle(s)/number of right side cusps), (2) lateral teeth (inner cusps/pronounced denticle/outer cusps), (3) marginal teeth (number of cusps on inner marginal tooth + number of cusps on outer marginal tooth).

Museum Abbreviations

- ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania
 BMNH The Natural History Museum, London, U.K.
 MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
 USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 ZMB Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University, Berlin, Germany

RESULTS

Hemisinus Swainson, 1840

Hemisinus Swainson, 1840: 341

Tania Gray, 1840: 148 [not available: *nomen nudum*]; not made available by Gray (1842: 61, 90), or by H. Adams & A. Adams, 1854: 302.
Semisinus P. Fischer, 1885: 701 [invalid: unjustified emendation of *Hemisinus*].

Type Species: *Strombus lineolatus* W. Wood, 1828, by monotypy.

Remarks

In his *Supplement* to the *Index Testaceologicus*, Wood (1828: 13–14, pl. 4) illustrated some shells from Asia and the Antilles under the generic allocation of *Strombus*, with specific names based on the most characteristic attribute of their shells. On a later page of this work (1828: 42) and in a subsequent paper (Wood, 1829: 31) indicated that Lamarck would place some of these species in his freshwater genus *Melania* Lamarck, 1799. In order to clearly delimit groups, Swainson (1840) erected *Hemisinus* for neotropical shells characterized by a “*melanid*” shape, but with the base of the aperture contracted and emarginated, in addition to a crenated outer lip. Fischer (1885) suggested *Semisinus* (*semi* = half, *sinus* = notch) as an emendation of *Hemisinus*, with Johnson & Fox (1891) returning to the use of *Hemisinus*. *Tania* Gray, 1840, was a *nomen nudum* when first proposed, and later sunk by Gray himself into the synonymy of *Hemisinus* (Gray, 1847: 153). *Haemisinus* was an incorrect subsequent spelling by Rotarides (1933) used

for a Pleistocene fossil from Hungary (and an incorrect usage for species of *Fagotia* Bourguignat 1884), and therefore has no standing in nomenclature.

Distribution

Greater Antilles (Jamaica and Cuba), Central America, Lesser Antilles (Barbados), and South America (Fig. 1). Nuttall (1990) also assigned fossil shells from the Paleogene and Neogene of Colombia, Ecuador and Peru to this genus.

Hemisinus lineolatus (W. Wood, 1828)

Strombus lineolatus W. Wood, 1828: 13, pl. 4, fig. 11.

Synonym: *Hemisinus buccinoides* Reeve, 1860: pl. 1, fig. 3a, b.

Other references

Melania lineolata – W. Wood, 1829: 31; Gray in Griffith & Pidgeon, 1833: pl. 13, fig. 4 [*non Melania lineolata* Gray in Griffith & Pidgeon, 1833: pl. 14, fig. 4]; Gray, 1847: 153; Philippi, 1848: 33, pl. 5, fig. 10; Jousseaume, 1889: 233; Cossmann, 1909: 150; Morrison, 1954: 376; Vega & Perrilliat, 1992: 604.

Hemisinus lineolata – Swainson, 1840: 341.

Melanopsis lineolata – C. B. Adams, 1849: 45; 1851: 187; Hanley, 1854–1858: pl. IV, fig. 29; Bland, 1861: 24; Orcutt, 1928: 12.

Melanopsis lineata – Poey, 1851: 399; 1856: 3
Hemisinus lineolatus – Gray, 1857: 103; H. Adams & A. Adams, 1854: 302, pl. 32, fig. 2a, b; Chenu, 1859: 291, fig. 1995; Reeve, 1860: plate 1, fig. 4a, b; Brot, 1878: 373, pl. 38, fig. 6, 6a–e; Kobelt, 1882: 131; Johnson & Fox, 1891: 34; Henderson, 1894: 33; Ihering, 1901: 672; Ihering, 1909: 311; Vernhout, 1914: 36; Baker, 1930: 30; Pain, 1956: 103; Nuttall, 1990: 239, figs. 224–226; Glaubrecht, 1996: 185.

Hemisinus (Basistoma) lineolatus – Brot, 1862: 61.

Melania (Hemisinus) lineolata – Martens, 1873: 51, 60.

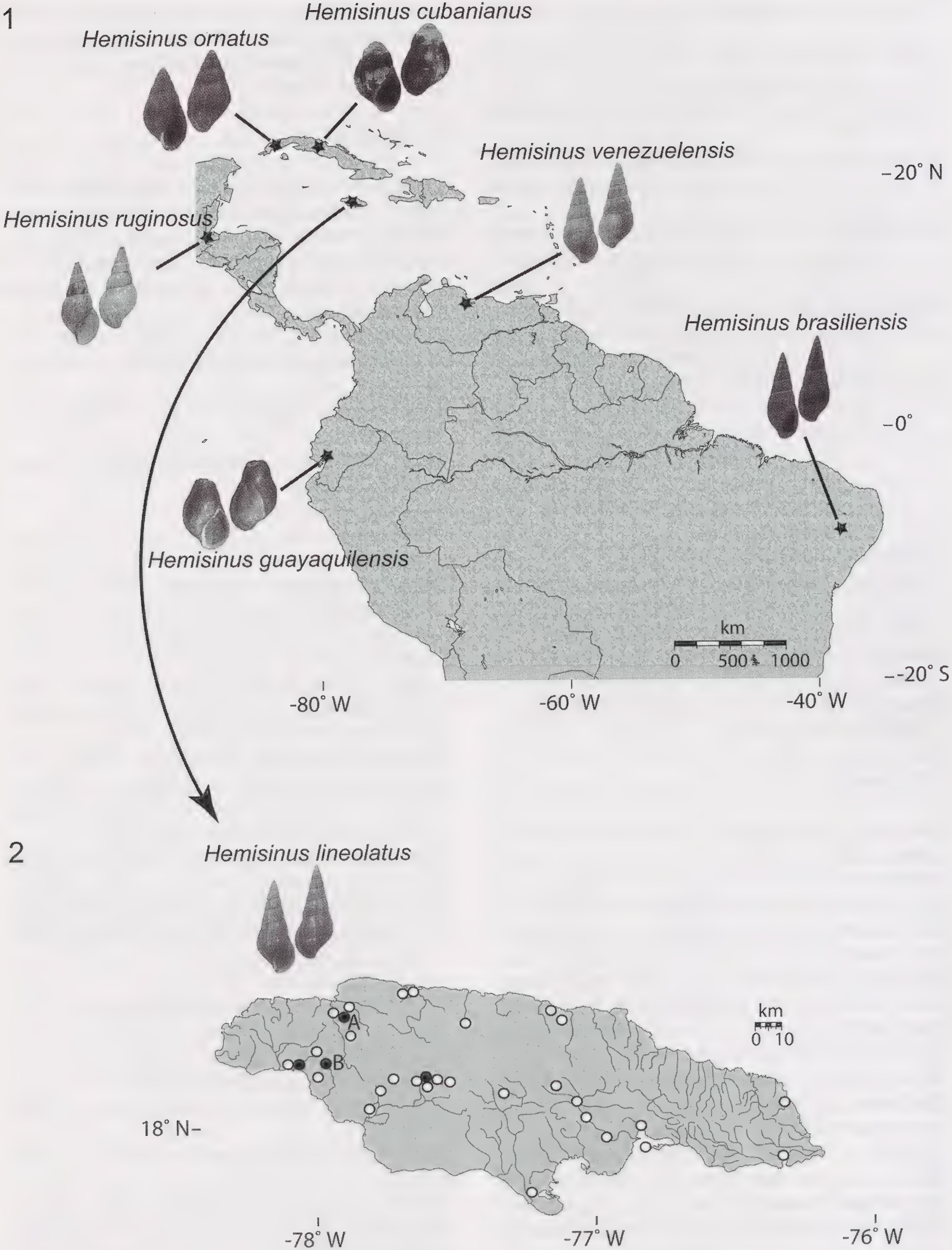
Semisinus lineolatus – Fischer, 1885: 702.

Semisinus lineolata – Vendryes, 1899: 13.

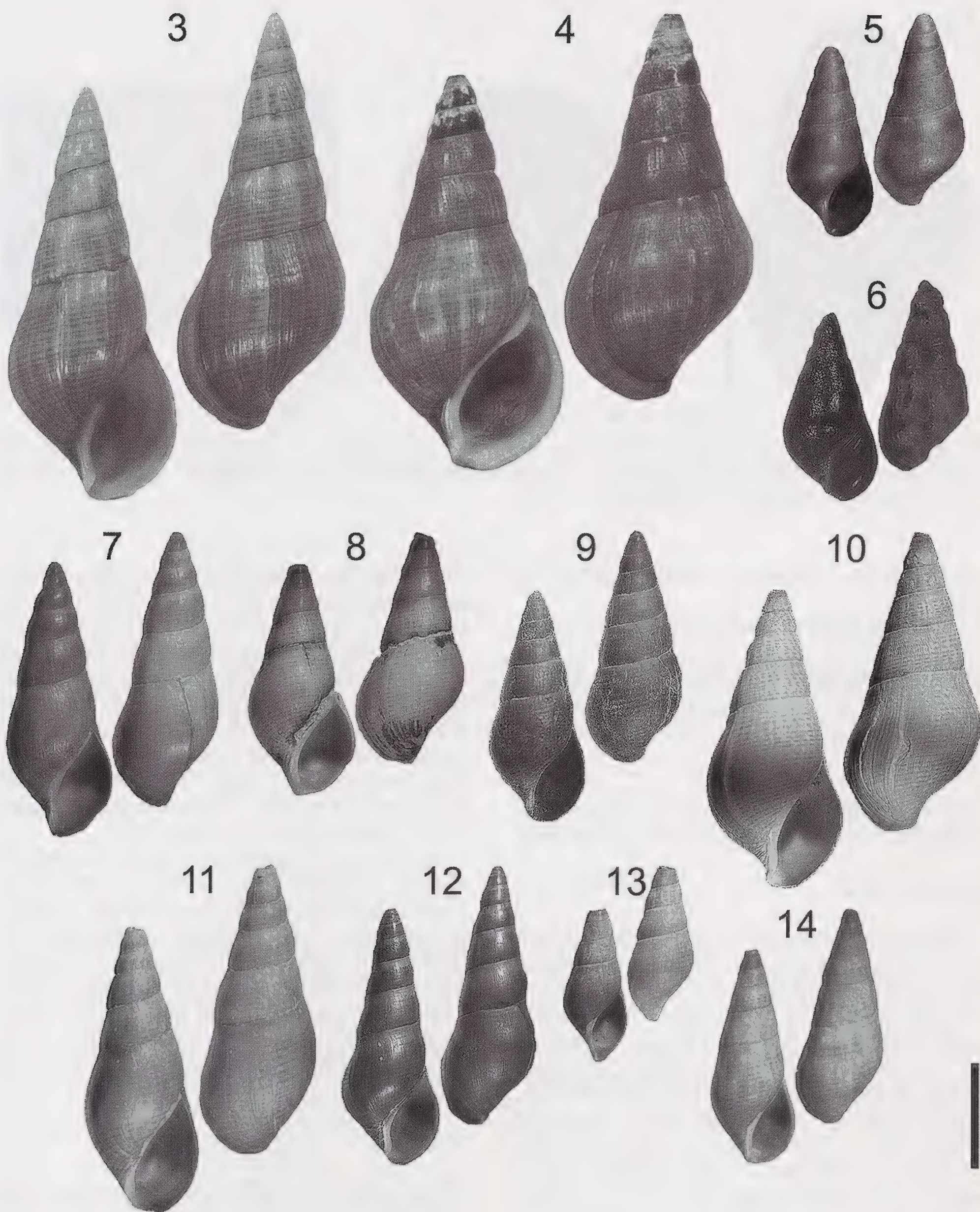
Melanopsis lineolatus – Vendryes, 1899: 13.

Hemisinus (Hemisinus) lineolatus – Thiele, 1928: 401; 1929: 201; Wenz, 1939: 718, fig. 2075; Jaeckel, 1969: 814, pl. 3, fig. 70.

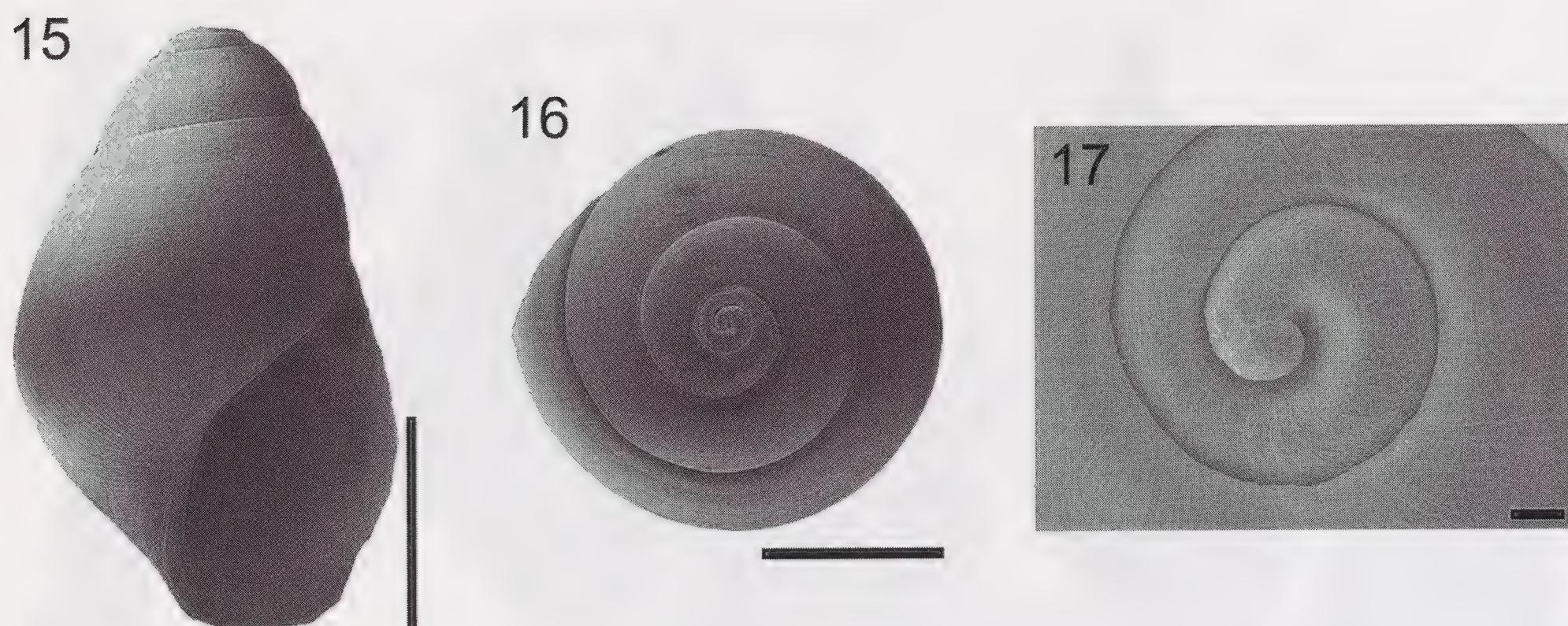
Aylacostoma (Hemisinus) lineolatum – Morrison, 1951: 9; 1954: 376.



FIGS. 1, 2. Distribution of *Hemisinus* Swainson, 1840. Not all nominal taxa shown. FIG. 1: *Hemisinus* spp.; FIG. 2: Occurrence of the type species *Hemisinus lineolatus* (W. Wood, 1828) on Jamaica; see text for details. ○ = museum shell material; ● = alcohol preserved material examined here for anatomy and histology; A, Anchovy Gully (ANSP 12087H-I); B, Black River, St. Elizabeth parish (ZMB 107126).



FIGS. 3–14. *Hemisinus* spp. FIG. 3: Lectotype of *Hemisinus lineolatus* (W. Wood, 1828) (BMNH 1984206/1); FIG. 4: Lectotype of *Hemisinus buccinoides* Reeve, 1860 (BMNH 1984208); FIGS. 5–14: Museum specimens of *Hemisinus lineolatus* from Jamaica; shells arranged from west to east. FIG. 5: Westmoreland Parrish (USNM 127820); FIG. 6: St. James Parrish (ANSP 120871); FIG. 7: St. Elizabeth Parrish (USNM 397352); FIG. 8: Trelawny Parrish (USNM 395818); FIG. 9: Manchester Parrish (USNM 345479); FIG. 10: St. Ann Parrish (USNM 395800); FIG. 11: Clarendon Parrish (USNM 395751); FIG. 12: St. Catherine Parrish (USNM 453971); FIG. 13: St. Andrew Parrish (USNM 378057); FIG. 14: Portland Parrish (USNM 712035). Scale bar = 1 cm.



FIGS. 15–17. Embryonic shell of *Hemisinus lineolatus* from brood pouch (ANSP 12087H). FIG. 15: Apertural view. Scale bar = 300 μ m; FIG. 16: Apical view. Scale bar = 200 μ m; FIG. 17: Initial whorl of embryonic shell, apical view. Scale bar = 50 μ m.

Aylacostoma lineolata – Simone, 2006: 82, pl. 199.

Hemisinus (*Basistoma*) *buccinoides* – Brot, 1862: 61.

Hemisinus lineolatus var. *buccinoides* – Kobelt, 1882: 131.

Type Locality

Strombus lineolatus: none given in the original description. *Hemisinus buccinoides*: Jamaica.

Type Material

Strombus lineolatus: Lectotype (Fig. 3) and six paralectotypes BMNH 1984206/1-7 Original label: front “*lineolatus* Wood, Hab. ?; *H. lineolata*; W. Sup. t. 4, f. 11; g. a. k., t. 13, f. 14; Holotype”; back “*Hemisinus lineolatus* Wood, Type, Hab. ?, Gray Collection”. Additional label: “BMNH ZD 1984206, Lectotype of *Strombus lineolatus* Wood 1828 [Type species of *Hemisinus* Swainson 1840], Hab. ? [Caribbean], Described and figd Nuttall, C.P. 1990. *Bull. Br. Mus. Nat. Hist.*, (Geol.) 45 (2). Pp. 238–240, figs. 224a, b. PTO. Wood 1828: pl. 4 [*Strombus* fig 11]– p. 42 [*Melania lineolata*], see Nuttall 1990 for full synonymy”.

The original description is silent with respect to the number of specimens examined and does not contain a (holo)type designation. The height of a single shell was provided ($h = 1\frac{1}{2}$ inches [3.81 cm]). A lectotype (Fig. 3) was designated by Nuttall (1990) on the basis

that it was the largest specimen and matched the size provided in the original description. In contrast to Nuttall’s (1990: 240) statement that this sample is composed of “*four unlocalized Recent shells*”, we found seven specimens (Lectotype and six paralectotypes). The discrepancy in reported numbers of specimens herein and in Nuttall is explained by an accompanying label stating: “*Thought to be a lot of 4 shells, 3 smaller shells later found under cotton wool – CP Nuttall May 1995*”.

Hemisinus buccinoides (Fig. 4): Lectotype BMNH 1984208. Original label: “*Hemisinus* [Type of *buccinoides*] *buccinoides* Rve. Jamaica (?), Jamaica, M. C.; Holotype”. Additional label “BMNH ZD 1984 208 Holotype of *Hemisinus buccinoides* Reeve 1860 = *H. lineolatus* (Wood 1828), Described and figd Nuttall, C.P. 1990. *Bull. Br. Mus. Nat. Hist.*, (Geol.) 45 (2). Pp 239–240, fig 226; Reeve Conch Icon pl. 1, fig. 3a, b)”.

Remarks

The authorship of *Strombus lineolatus* has been the subject of several discussions. The species name has been attributed to Gray, to Griffith in Cuvier, to Gray in Griffith & Pidgeon, to Wood in Gray, or to Gray in Wood. Nevertheless, as confirmed by Petit & Coan (2008), the name was validly established by William Wood (1774–1857), who copied it from labels prepared by J. E. Gray in the British Museum.

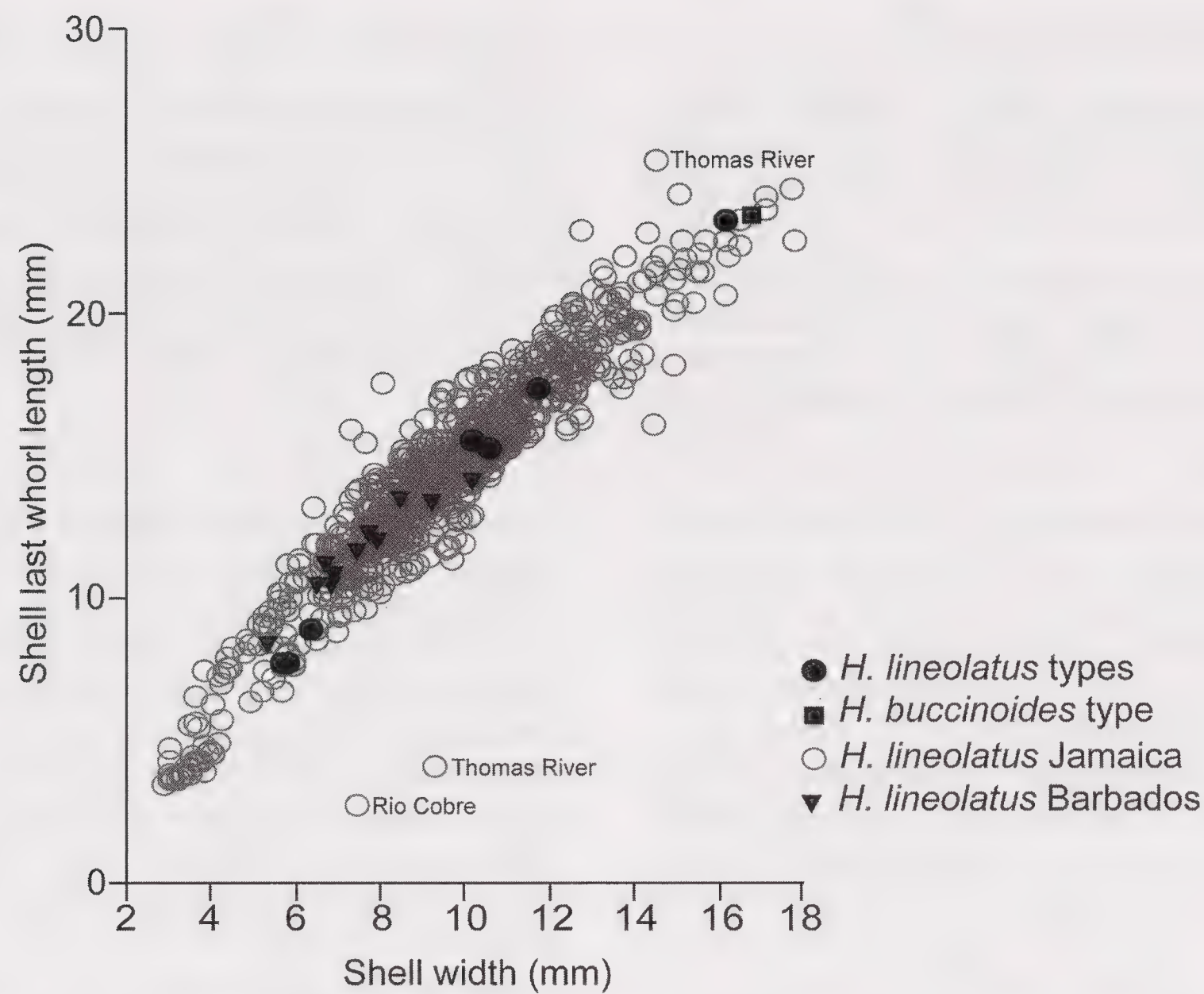


FIG. 18. Scatterplot of Jamaican *Hemisinus* shell width and last whorl length (outliers indicated). ● = types of *H. lineolatus* (BMNH 1984206/1-7); ■ = lectotype of *H. buccinoides* (BMNH 1984208); ○ = other Jamaican material examined; ▼ = *H. lineolatus* from Barbados (USNM 272287).

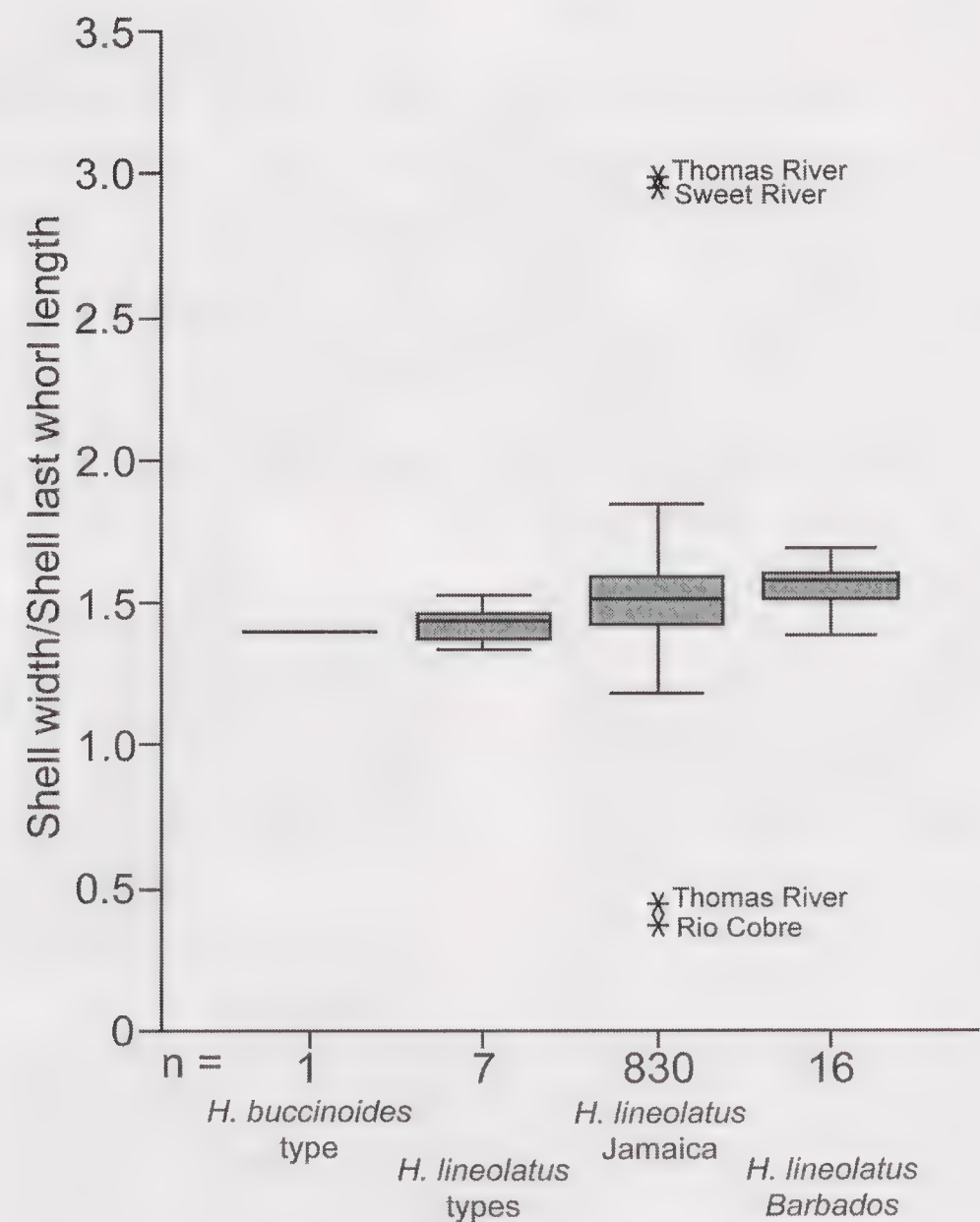


FIG. 19. Boxplot comparative analysis of shell width and last whorl length for *Hemisinus* shells from Jamaica (outliers indicated).

Additional Material Examined

Jamaica: (ANSP 26797, 26800, 122992, 123029; BMNH 1845.9.16.63, 1857.12.1.1135, 36, 37, 39, 41, 20070080, 20070085; ZMB 113036, 113037, 113038, n = 70). Westmoreland: Savanna-La-Mar (USNM 792463, n = 3); Ditch near Savanna-La-Mar (USNM 127820, n = 2; Fig. 5); Sweet River: near Savanna-La-Mar (USNM 127799, n = 8); Water Wheel (ANSP A12088A, A12088B; MCZ 195360, n = 10); Mackfield: Williamsfield Cave (BMNH 29.1.1907, n = 24); Mt. Pleasant (USNM 127821, n = 1). St. James: Anchovy Gully (ANSP A12087H, A12087I, n = 25; Fig. 6); Great River (USNM 127827, n = 2); Great River, first falls from the mouth (ANSP 153283, 159740; ZMB 113039, n = 7); Great River, seven miles south of Montego Bay (USNM 792464, n = 3); Montpellier (USNM 168599, 453972, n = 4); Spring Mount: (ANSP 160299, n = 25), Montego Bay: Mt. Horibb (MCZ 88922, n = 4). St. Elizabeth: Route A-2 about 2 mi. NE Middle Quarters (ANSP 375045, n = 11); Ipswich (USNM 168598, 453973, n = 11); Accompong River, Hole Cockpit (USNM 376369, n = 17); 3 miles north of BalACLava, Opfor Cave (USNM 374547, 396156, n = 9); Wallingford River (USNM 210911, n = 2); BalACLava (ANSP 226265, n = 2); Near BalACLava: Cave at sink of One Eye River (USNM 397352, 397082, 427066, 427096, n = 78; Fig. 7); Harbor Shore, Black River (USNM 427037, n = 1); Black River (MCZ 172867, n = 12). Trelawny: Falmouth: Bush Cay (USNM 395818, n = 8; Fig. 8); Near Westwood High School (USNM 399377, n = 1); Dornach River (ANSP 157713, n = 19). Manchester: One Eye River (USNM 374377, 375429, 375479, 398576, n = 62; Fig. 9); Middlesex, Black River north of Oxford (ZMB 107126, n = 5); Oxford Cave: top of hill over Oxford Cave, 3 mile north (USNM 398577, n = 50). St. Ann: Rio Bueno, near Dornach Power House (USNM 395800, 427097, n = 13; Fig. 10); St. Ann's Bay: Roaring River (ANSP 157714; USNM 127826, 453968, n = 46); Fern Gully (ANSP 160259; USNM 511960, 526273, n = 51). Clarendon: Frankfield (USNM 400639, n = 25); Rio Minho (USNM 395751, n = 11; Fig. 11); Portland (MCZ 195361, n = 6). St. Catherine: 1 mile from Ewarton to Moneague (USNM 396044, n = 1); Bog Walk (ANSP 61889; BMNH 20070081; USNM 127351, 127822, 453971, 394750, 394861, 395486, 395529, 427094, 427095, n = 111; Fig. 12); Bog Walk: Thomas

River (USNM 427093, n = 31); Rio Cobre (ANSP 124742, 157271, 26798; USNM 700721, n = 79); Spanish Town: Canal drift (USNM 395743, n = 5). St. Andrew: Port Royal (USNM 442331, n = 1); Hunts Bay (USNM 378057, n = 1; Fig. 13). Portland: Priestmans River (USNM 712035, n = 9; Fig. 14). St. Thomas: Morant Bay (MCZ 115072, n = 8) (Fig. 2). Lesser Antilles: Barbados (USNM 272287, n = 16).

Distribution

The first time that *Hemisinus lineolatus* was reported from Jamaica was in Philippi (1848), wherein a shell that fits the illustration in Wood's original description is depicted. Afterwards, Poey (1851, 1856) restricted the species to the island, a view which is subsequently followed (Bland, 1861; Arango y Molina, 1865; Brot, 1878; Johnson & Fox, 1891; Henderson, 1894; Vendryes, 1899; Orcutt, 1928; Nuttall, 1990; Glaubrecht, 1996; Townsend & Newell, 2006). However, according to statistical analyses here performed (PCA, Scatter- and Box-plot), shells from Barbados (Lesser Antilles) are not different from those from Jamaica (Figs. 18, 19). Thus, until suitable material for anatomical studies of the Barbados specimens is available, the species distribution cannot be restricted to Jamaica.

On the other hand, *H. lineolatus* has been also reported in British Guiana and Surinam (Pain, 1956). Its presence, argued by Pain as man-made introduction, is not supported by Nuttall (1990), because the distribution data is both suspect and anomalous. Molecular analyses of specimens from continental America similar in shell shape and appearance with *H. lineolatus* showed that they are genetically distinct (Gomez, unpubl. data).

TABLE 1. Shell measurements (in millimeters) of embryonic shells (n = 7) obtained from the brood pouch of *Hemisinus lineolatus* from Jamaica. Abbreviations: dp, protoconch diameter; he, embryonic shell height; SD, standard deviation; we, embryonic shell width.

<i>H. lineolatus</i>	he	we	dp
range	2.42–4.88	2.18–3.17	0.29–0.74
mean	3.61	2.51	0.46
SD	0.90	0.40	0.15

Description

Shell: Embryonic Shell. Globose, smooth, faint axial and spiral lines, suture shallow, two to three whorls (Fig. 15). Color yellow or light brown. Apical cap smooth to only very weakly wrinkled, 1.25 whorls (Figs. 16, 17). Ranging in height from 2.4–4.8, mean = 3.61, standard deviation (SD) = 0.9 (n = 7) (Table 1).

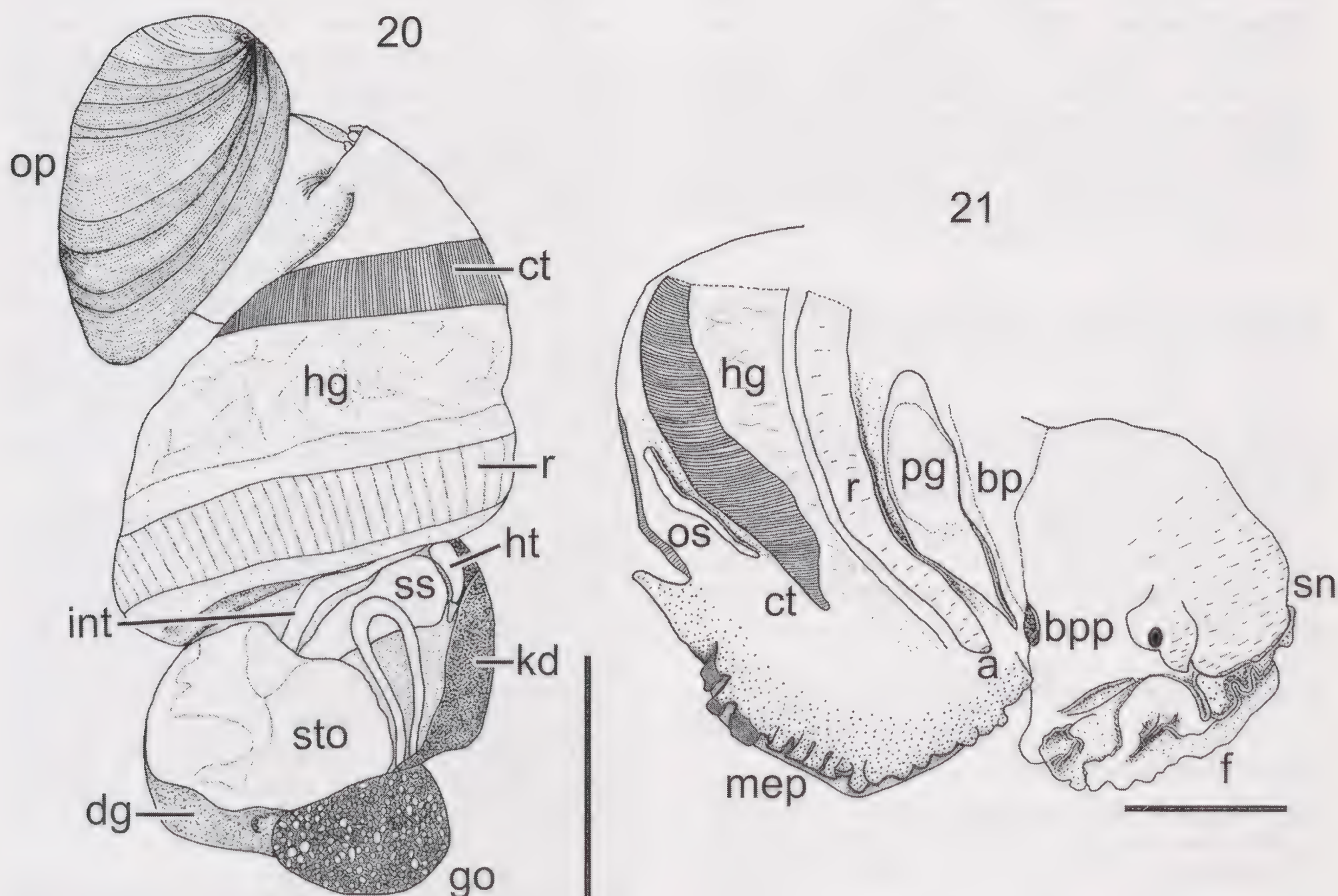
Adult Shell. Conic, thin but solid, usually with apex not eroded, comprising five to six whorls. Spire with flattened whorls; body whorl inflated. Suture narrow and subsutural depression shallow, both forming colored band. Shell smooth, with faint axial and spiral growth lines. Color from yellow-brown to black, with reddish, spiral, interrupted color bands. Aperture ovate, angled above, expanded below, inside white (Figs. 3–14).

Maximum shell height, 42.7 mm, minimum shell height, 4.3 mm, mean = 22.3 mm, SD =

6.1 mm (n = 830) (Table 2). First two principal components explaining 93.137% of variance (Table 3). PC1 having high loading values for shell width and last whorl length; PC2 having high loading value for whorl number (Table 3).

Scatterplot and boxplot comparisons showing no significant morphometric differences among Jamaican populations nor between Jamaican and Barbados populations (Figs. 18, 19).

External Anatomy. Operculum (Fig. 20) ovate, corneous, reddish-brown; paucispiral, with small subterminal nucleus of about two whorls. Animal pale yellow, with brown or dark grey patches on tentacles, snout and anterior part of foot (Fig. 21). In females, brood pouch pore present on right side of head-foot, close to tip of pallial oviduct (Fig. 21). Snout short and broad. Tentacles broad, tapering, shorter than snout when retracted. Mantle edge with



FIGS. 20, 21. Anatomy of *Hemisinus lineolatus* (Westmoreland, Jamaica, ANSP 12088A-B). FIG. 20: External anatomy, ventral view. Scale bar = 5 mm; FIG. 21: Anatomy of mantle cavity and brood pouch. Scale bar = 2 mm. Abbreviations: a, anus; bp, brood pouch; bpp, brood pouch pore; ct, ctenidium; dg, digestive gland; f, foot; go, gonad; hg, hypobranchial gland; ht, heart; int, intestine; kd, kidney; mep, mantle edge papillae; op, operculum; os, osphradium; pg, pallial gonoduct; r, rectum; sn, snout; ss, style sac; sto, stomach.

TABLE 2. Shell measurements of type specimens of *Hemisinus lineolatus* (lectotype BMNH 1984208) and *H. buccinoides* (lectotype BMNH 1984206/1), and Jamaican specimens of *H. lineolatus* from museum collections (n = 830). Abbreviations: h, shell height; la, aperture height; ltw, last three whorls; lwl, last whorl length; SD, standard deviation; w, shell width; wa, aperture width; wn, whorl number.

Species	h	w	la	wa	lwl	ltw	wn
<i>H. lineolatus</i>							
lectotype	39.78	16.19	16.50	8.20	23.31	32.30	9
<i>H. buccinoides</i>							
lectotype	37.17	16.78	17.91	8.45	23.43	31.69	6
<i>H. lineolatus</i> Jamaica							
range	4.35–42.77	2.90–14.56	2.75–17.02	1.34–7.47	3.46–25.40	4.35–36.06	3–6
mean	22.35	9.42	10.14	4.20	14.20	19.20	5.39
SD	6.10	2.60	2.82	1.58	3.76	5.38	1.31

13–21 papillae (n = 17; mean = 17; SD = 2.01) (Fig. 21). Mantle cavity extending approximately one whorl. Hypobranchial gland well developed, thick, with transverse grooves (Fig. 20). Ctenidium straight, long, with attached base of leaflets, narrow anteriorly and broad posteriorly (Fig. 21). Osphradium conspicuous, near anterior end of ctenidium, slightly curved, short, about one-third of ctenidium in length (Fig. 21). In some specimens (Black River, ZMB 107126, n = 5), osphradium slightly more than twice average length.

Alimentary System: Foregut. Buccal mass robust, pear-shaped (Fig. 22). Radular sac

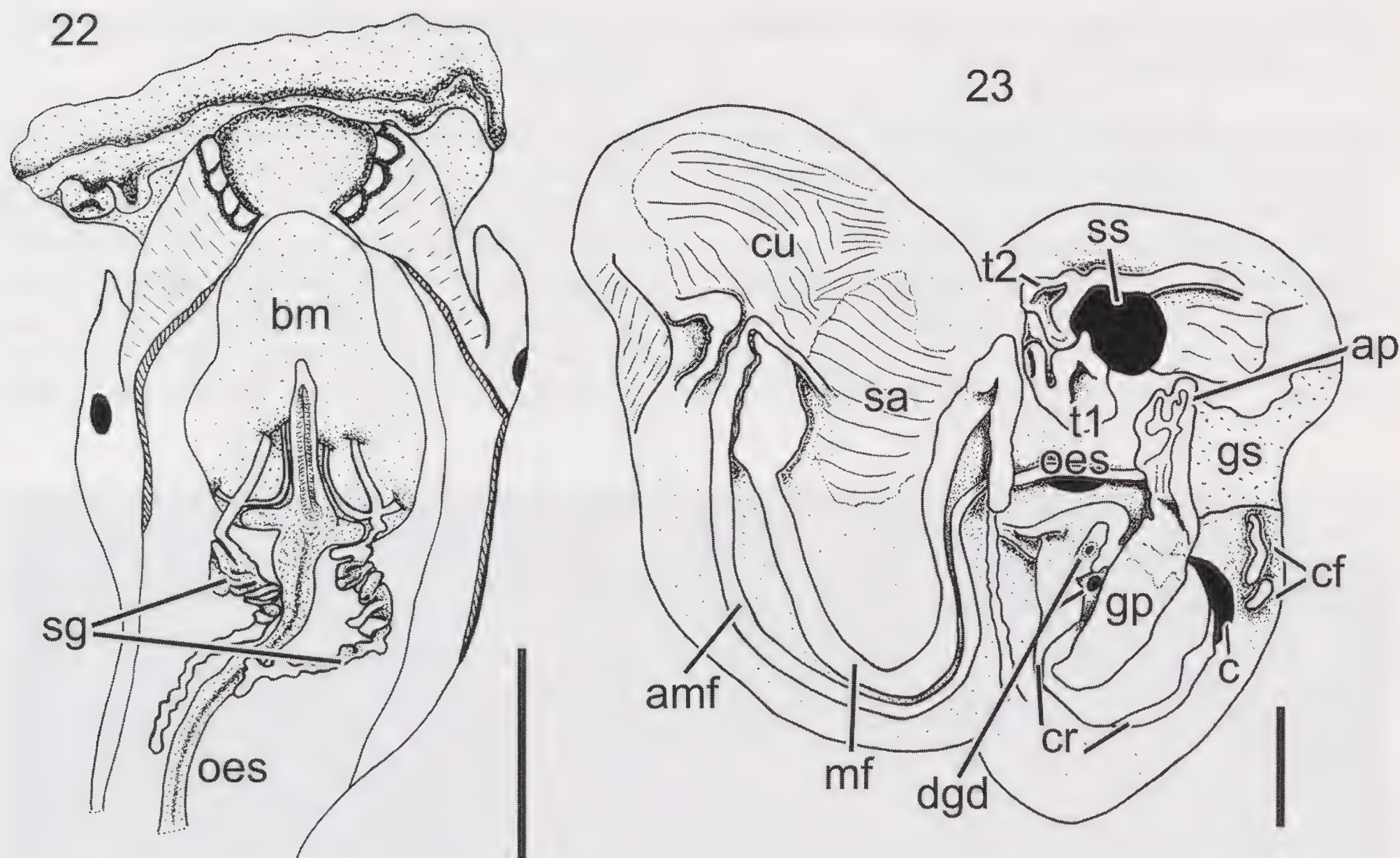
short, slightly curving behind, reaching base of anterior esophagus (Fig. 22). Radula with 140 rows (average of n = 5). Rachidian (Figs. 24–27) pentagonal, approximately twice broader than high, with concave anterior edge, v-shaped base. Cutting edge bearing rectangular, rounded central cusp, with two to three rounded (Fig. 26) or pointed (Fig. 27) denticles on either side (2–3/1/2–3). Rachidian with basal denticle at each outer corner. Lateral teeth bearing broad, squarish central cusp flanked by two to three short, rounded to pointed cusps on either side (2–3/1/2–3) (Figs. 26, 27). Marginal teeth (Figs. 28, 29) long, spatulate, with narrow flanges along shaft. Broad, rounded cutting edge bearing four to five short rounded denticles (Fig. 28), or up to eight slender, fringe-like denticles (Fig. 29).

Thick buccal retractors inserting laterally near middle of buccal mass, extending to lateral walls of cephalic hemocoel adjacent to cerebral ganglia. Salivary glands (Fig. 22) opening dorso-laterally to buccal cavity. Glands long, tubular, passing through nerve ring, extending short distance posteriorly; left salivary gland passing above supra-esophageal ganglion. Mid-esophageal gland absent.

TABLE 3. Principal component analysis on the correlation matrix of *Hemisinus lineolatus* on seven shell parameters (n = 830). Abbreviations: h, shell height; la, aperture height; ltw, last three whorls; lwl, last whorl length; PC, principal component; w, shell width; wa, aperture width; wn, whorl number.

PC	Eigen value	Variance (in %)	Data	Component loadings	
				PC 1	PC 2
1	5.51109	78.73	h	-0.4133	0.1335
2	1.00851	14.407	w	-0.4135	-0.1138
3	0.23881	3.4116	la	-0.4124	-0.1115
4	0.13618	1.9455	wa	-0.3849	-0.1634
5	0.04719	0.6741	lwl	-0.4176	-0.0644
6	0.04038	0.5769	ltw	-0.3934	0.0696
7	0.01784	0.2549	wn	-0.1046	0.9597

Midgut (Fig. 23). Esophagus opening to midgut floor at left. Stomach roof with large, oval sorting area and small, irregularly folded cuticularized anterior portion. Marginal fold with broad U-shaped anterior tip; fold extending from major typhlosole, alongside sorting area, around posterior end of stomach. Accessory marginal fold emerging from esophageal



FIGS. 22, 23. Digestive system of *Hemisinus lineolatus*. FIG. 22: Foregut morphology, dorsal view (Black River, Jamaica; ZMB 107126). Scale bar = 2 mm; FIG. 23: Midgut morphology, dorsal view (Westmoreland, Jamaica; ANSP A12088A). Scale bar = 1 mm. Abbreviations: amf, accesory marginal fold; ap, accessory pad; bm, buccal mass; c, caecum; cf, caecal folds; cr, crescentic ridge; cu, cuticle; dgd, digestive gland duct; gp, glandular pad; gs, gastric shield; mf, maginal fold; oes, esophagus; sa, sorting area; sg, salivary glands; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

aperture, paralleling marginal fold around posterior end of stomach. Crystalline style pocket rounded and small. Gastric shield narrow. Glandular pad large, rounded, more than twice as long as broad. Large, textured accessory pad present at anterior end of glandular pad at left. Crescentic ridge emerging behind esophageal aperture, extending posteriorly around glandular pad, fusing to glandular pad above caecum behind gastric shield; caecum shallow, extending short distance under glandular pad. Two caecal folds opposite caecum; posterior fold half size of anterior fold. Paired digestive gland ducts opening to crescentic groove at left of glandular pad. Style sac and intestinal groove completely separated by fused typhlosoles.

Hindgut. Proximal intestine passing around anterior tip of style sac, forming U-curve in front of gastric chamber partially overlying style sac (Fig. 20), continuing anteriorly alongside kidney, entering pallial roof above pallial gonoduct, terminating with simple anus near mantle edge (Fig. 21).

Reno-Pericardial System. Kidney large, wide, reaching base of mantle cavity between intestine and ctenidium, bounded behind by digestive gland and style sac (Fig. 20). Lumen subdivided into chambers. Pericardial coelom deep, narrow, extending posteriorly under kidney along style sac.

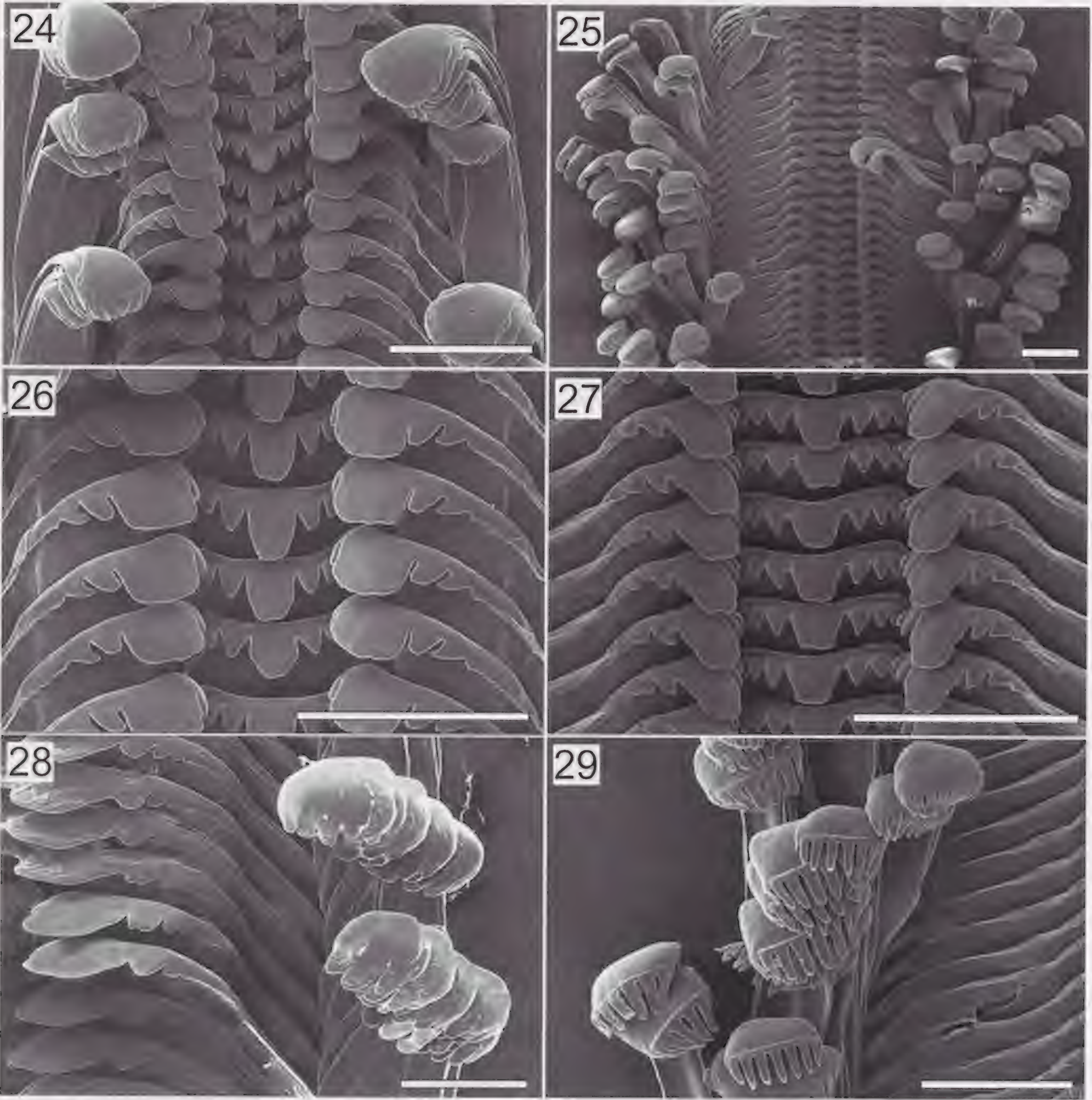
Nervous System (Figs. 30, 31): Circum-esophageal nerve ring lying immediately behind buccal mass. Cerebral ganglia above esophagus, connected by short commissure; each ganglion producing six nerves. Pleural ganglia behind and below cerebral ganglia, forming almost one mass on each side (Fig. 30). Two pedal ganglia united by short commissure, lying ventrally in foot, with three prominent accessory nerves (Fig. 31). Sub-esophageal ganglion closely adjacent to left pleural ganglion. Dialyneurous connection between right pleural and sub-esophageal ganglion (not shown). Long connective joining supra-esophageal ganglion and right pleural ganglion (Fig. 31). Statocysts with up to 50 angular statoconia, present dorsally and

behind pedal ganglia, with long connectives to cerebral ganglia (Fig. 30).

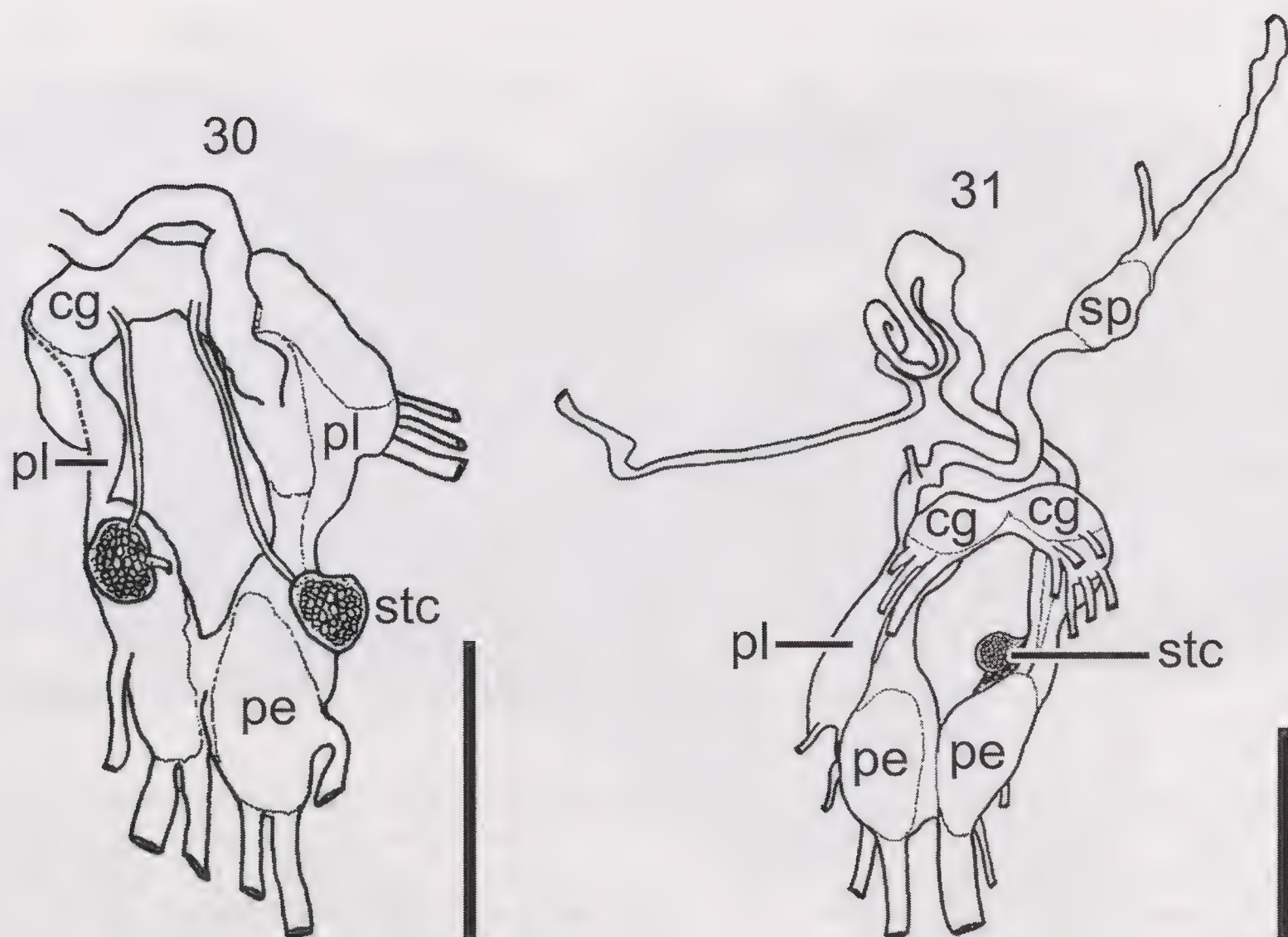
Reproductive System: Gonad (Fig. 20) developing from tip of visceral whorls to posterior end of stomach, overlying digestive gland; similar in general aspect in males and females. Visceral gonoduct emerging ventrally in both sexes. Sexual dimorphism determined by presence of brood pouch pore at right side of adult females' head-foot (Fig.

21). Gender ratio of 52% females and 48% males (n = 30).

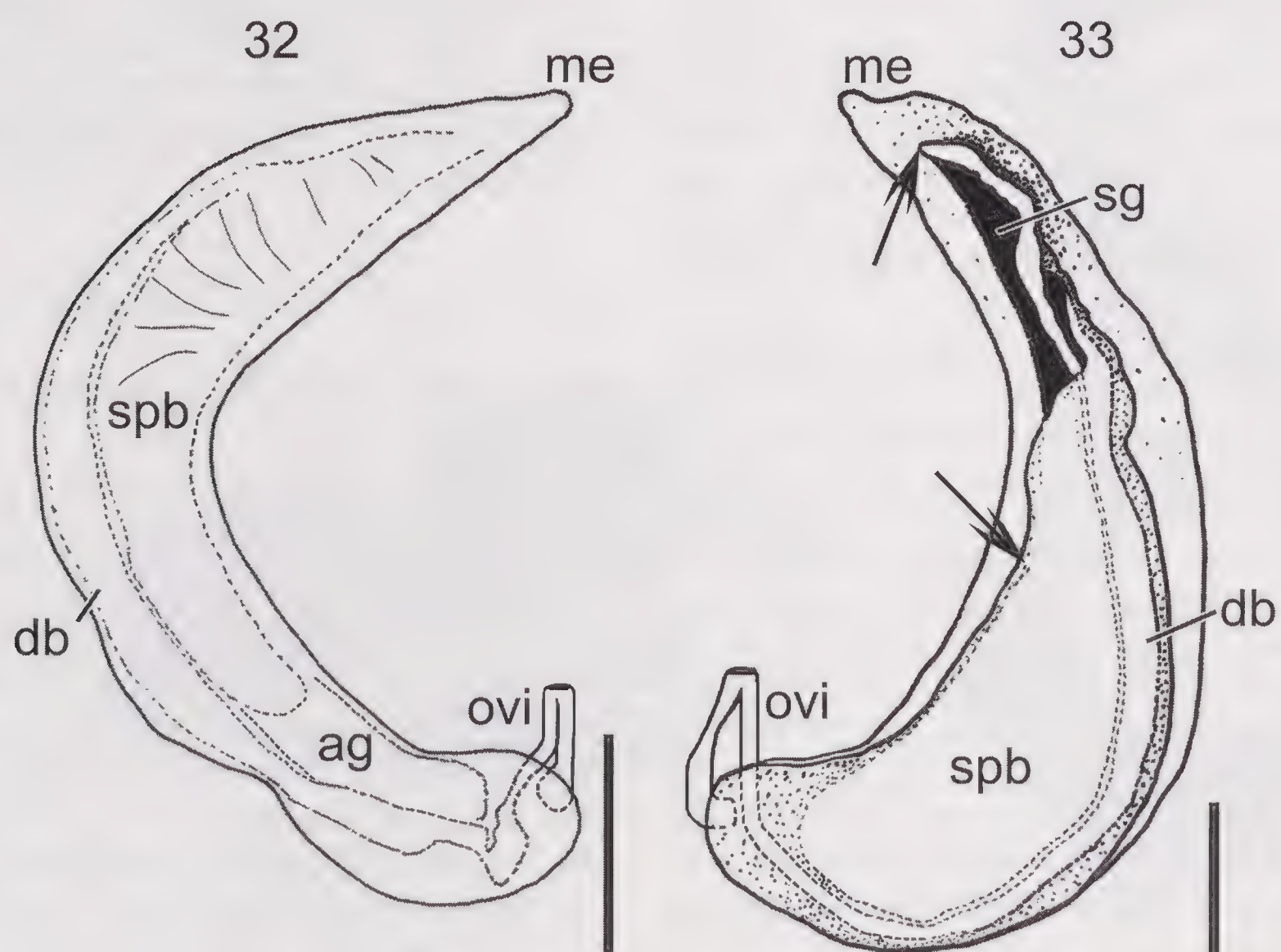
Female Reproductive System: Renal oviduct short, curved, thick (Fig. 32: ovi), with two branches; one branch entering pallial gonoduct posteriorly, second dorsal branch embedded in lateral lamina entering more anteriorly (Fig. 32). Pallial oviduct opening to mantle cavity through ventral slit along anterior half (Fig. 33: arrows). Pallial oviduct with



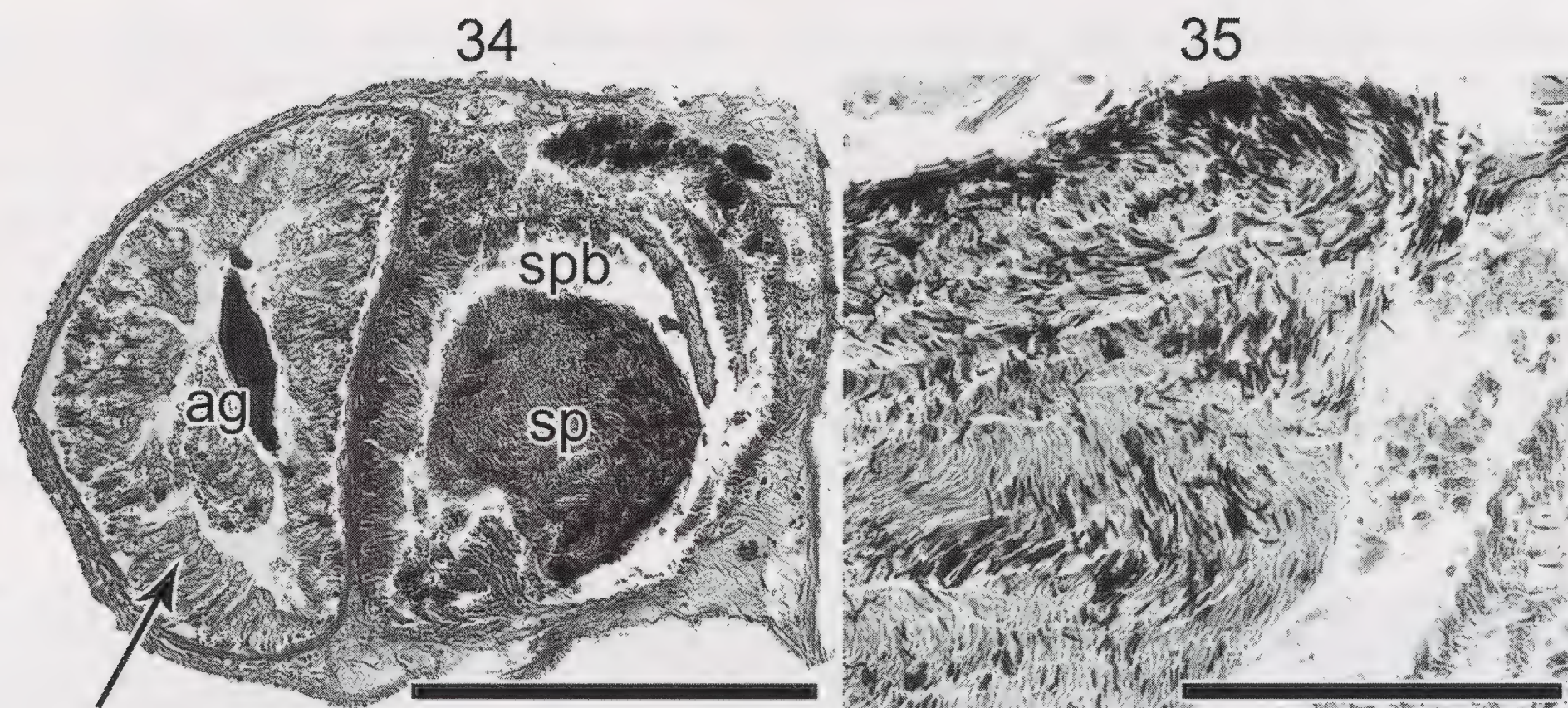
FIGS. 24–29, Radula of *Hemisinus lineolatus* from Jamaica. FIGS. 24, 25: Overview of radular ribbon. FIG. 24: ANSP 120781; FIG. 25: ZMB 107126. Scale bar = 100 μ m; FIGS. 26, 27: Detail of rachidian and lateral teeth. FIG. 26: ANSP 120781; FIG. 27: ZMB 107126. Scale bar = 100 μ m; FIGS. 28, 29: Detail of lateral and marginal teeth. FIG. 28: ANSP 120781. Scale bar = 50 μ m; FIG. 29: ZMB 107126. Scale bar = 100 μ m.



FIGS. 30, 31. Circum-esophageal nerve ring of *Hemisinus lineolatus*. FIG. 30: Circum-esophageal nerve ring, rear view (Westmoreland, Jamaica; ANSP 12088A); FIG. 31: Nerve ring, frontal view (Westmoreland, Jamaica; ANSP 12088A). Scale bars = 1 mm. Abbreviations: cg, cerebral ganglia; pe, pedal ganglia; pl, pleural ganglia; sp, supra-esophageal ganglion; stc, statocyst.



FIGS. 32, 33. Female pallial oviduct of *Hemisinus lineolatus* (Anchovy Gully, Jamaica, ANSP 12087H). FIG. 32: External, right lateral view of lateral lamina; FIG. 33: Internal view of lateral lamina (external wall, i.e. medial lamina, of albumen gland removed), arrows indicate extent of gonoduct opening to mantle cavity. Scale bars = 1 mm. Abbreviations: ag, albumen gland; db, dorsal branch of renal oviduct; me, mantle edge; ovi, renal oviduct; sg, sperm gutter; spb, spermatophore bursa.



FIGS. 34, 35. Histological detail of a female pallial oviduct of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 12087I; dorsal is uppermost). FIG. 34: Albumen gland with glandular epithelium (arrow) and spermatophore bursa with unorientated sperm. Scale bar = 0.5 μ m; FIG. 35: Detail of sperm in lumen of spermatophore bursa. Note darkly staining sperm heads. Scale bar = 0.125 μ m. Abbreviations: ag, albumen gland; sp, sperm; spb, spermatophore bursa.

unspecialized glandular epithelium anteriorly, and forming highly folded albumen gland posteriorly lined with tall, basophilic, prismatic cells (Fig. 34: arrow). Sperm gutter in lateral lamina beginning slightly back from anterior end of pallial oviduct, deepening posteriorly, enclosing entrance to spermatophore bursa at midpoint of gonoduct (Fig. 33). Gutter receiving dorsal branch of renal oviduct near entrance of bursa. Lumen of spermatophore bursa containing densely packed unorientated sperm (Figs. 34, 35).

Females with cephalic brood pouch extending posteriorly from brood pore on side of neck behind right eye to end of mantle cavity (Fig. 36). Lumen of brood pouch dorsal, above esophagus; lumen not compartmentalized (Figs. 37–44). Wall of brood pouch (Fig. 45) formed by thin layer of smooth muscle lined by thin layer of tall columnar cells with large, basal nuclei (Fig. 45). Brood pouch containing single large, shelled juvenile (ANSP 12087I, 12087H, Anchovy Gully; $n = 10$), or up to three juveniles of variable size (ZMB 107126, Black River; $n = 5$). Embryonic shells surrounded by thin epithelial tissue. No eggs or early developmental stages present.

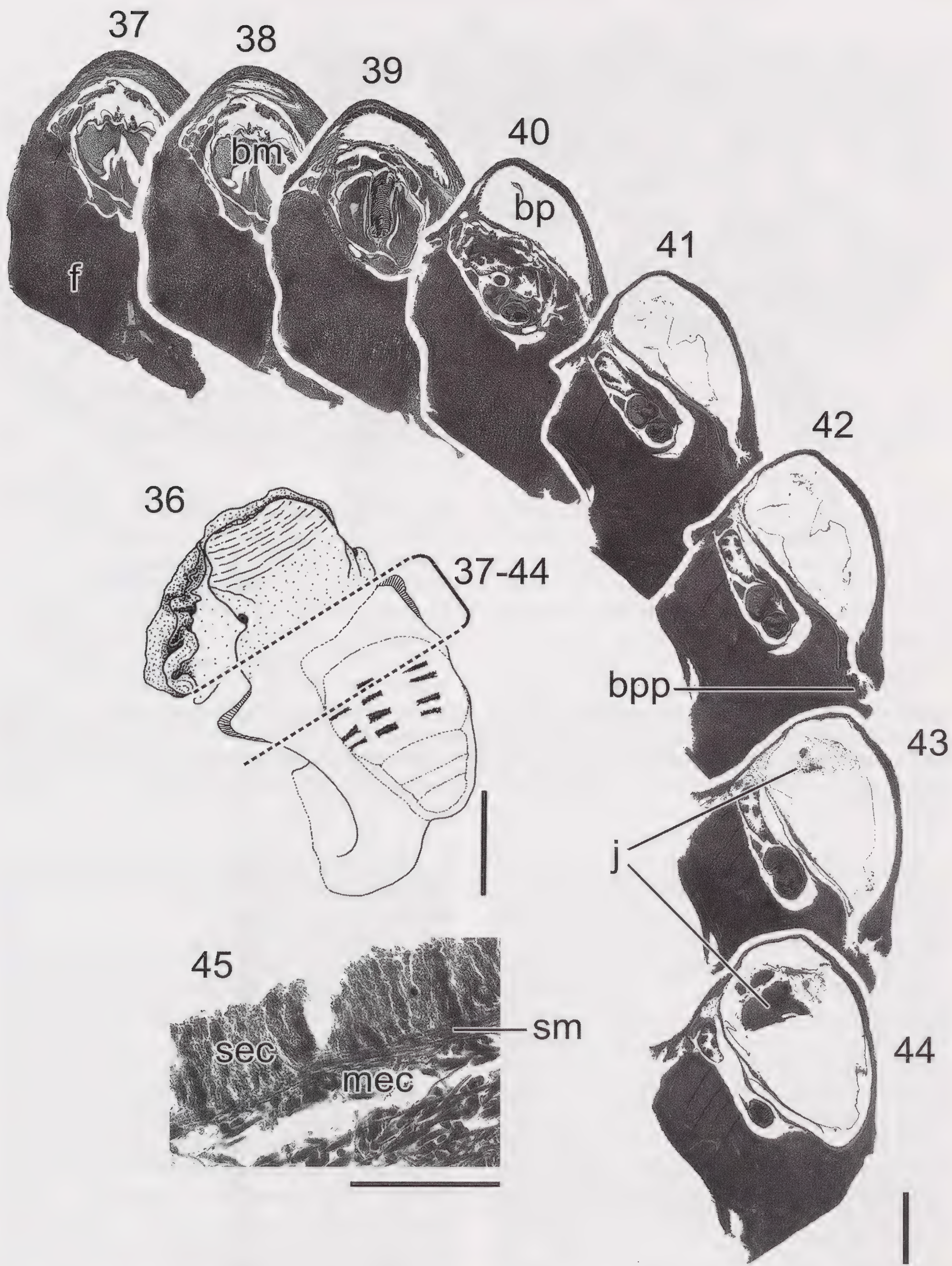
Male Reproductive System: Narrow vas deferens straight, entering posterior end of prostate near base of mantle cavity. Prostate opening to mantle cavity along entire

length except short, fused segment at base of mantle cavity (Figs. 46–56). Mid-dorsal portion of prostate forming short, glandular spermatophore forming organ. Organ terminating blindly posteriorly, communicating anteriorly with prostate lumen (Figs. 50–52). Organ lumen lined with tall prismatic epithelium (Fig. 57), containing unorientated sperm (Fig. 58: arrow).

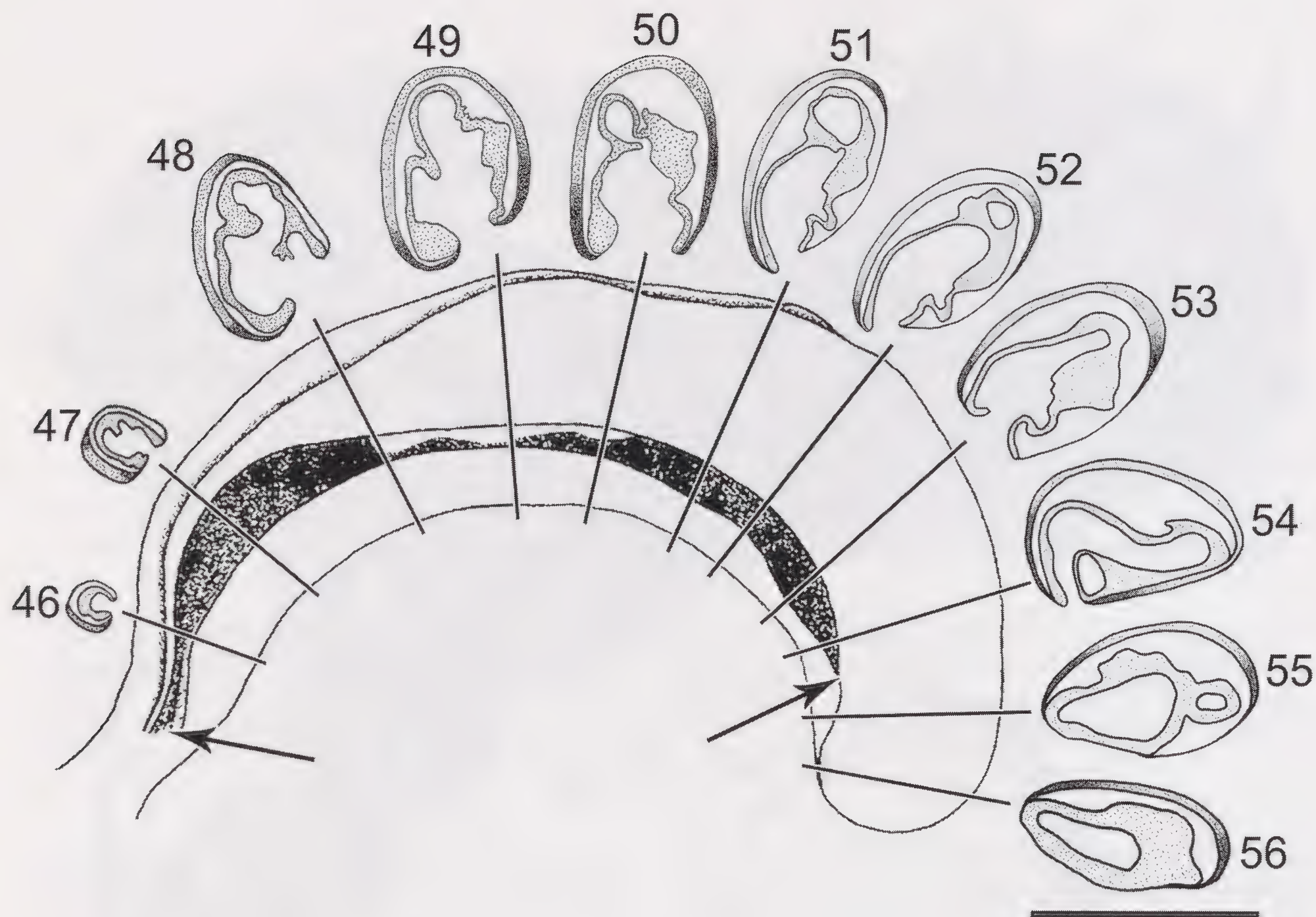
DISCUSSION

Intraspecific Variability in *Hemisinus lineolatus*

Hemisinus buccinoides was described by Reeve (1860: pl. 1, fig. 3a, b) for an unknown number of shells from Cuming's collection, the origin of which was thought to be Jamaican (Reeve, 1860). It was assumed by Brot (1878) and Simpson (1894) that *buccinoides* was a synonym of *lineolatus*. Shortly thereafter, the species name *buccinoides* disappeared from the literature, leaving only the name *lineolatus* for Jamaican Thiaridae. Comparative analyses of *Hemisinus* shell width and last whorl length through west-east and north-south gradients in Jamaica reveal neither patterns nor trends (data not shown). The lack of significant differences between shells of *H. lineolatus* and *H. buccinoides*, as demonstrated by graphical statistical analysis (Figs. 18, 19), supports this hypothesis.



FIGS. 36–45. Brood pouch anatomy of mature female of *Hemisinus lineolatus* (Anchovy Gully, Jamaica, ANSP 12087H). FIG. 36: Location of brood pouch. Scale bar = 1 mm; FIGS. 37–44: Histological sections of brood pouch from anterior (above) to posterior. Scale bar = 10 µm; FIG. 45: Detail of brood pouch wall (brood chamber is above). Scale bar = 1 µm. Abbreviations: bm, buccal mass; bp, brood pouch; bpp, brood pouch pore; f, foot; j, juvenile; mec, mantle floor epithelium; sec, columnar epithelium; sm, smooth muscle.

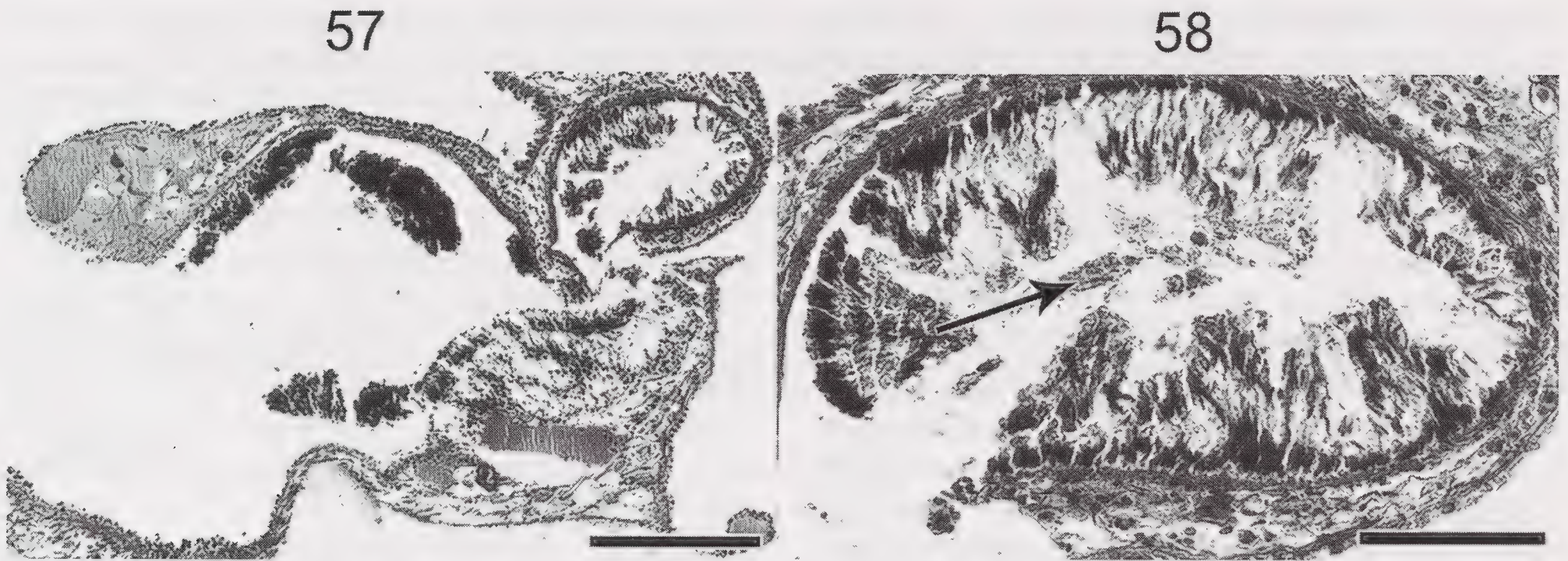


FIGS. 46–56. Male pallial gonoduct of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 12087I). Reconstruction of the internal anatomy with sections from anterior (left) to posterior. Arrows indicate extent of opening to mantle cavity. FIGS. 47–49: Main chamber with longitudinal folds building grooves; FIGS. 50–52: Spermatophore forming organ; FIG. 55: Vas deferens entrance to the prostate. Scale bars = 1 mm.

However, some anatomical differences were found between one population of the northwest Jamaican coast (Anchovy Gully, St. James parish, ANSP 12087I, H; $n = 10$) and one from the central part of the island (Black River, St. Elizabeth parish, ZMB 107126; $n = 5$) in the shape of radular teeth, osphradium length, length of the oviductal opening to the mantle cavity, and number of juveniles inside the brood pouch. Specimens from Anchovy-Gully show rounded radular denticles, an oviductal aperture that extends to the middle of the pallial gonoduct, and only one embryo in each brood pouch. Specimens from the Black River have pointed and slender radular denticles; the osphradium is twice as long as that of the Anchovy-Gully specimens; the oviductal aperture extends slightly beyond the middle of the gonoduct; and at least three juveniles of different size were found inside the brood pouch. However, adult and embryonic shell morphology, as well

as anatomy of the nervous system, male pallial gonoduct, and stomach showed no differences between the populations.

In gastropods, radular morphology and environmental conditions are highly correlated. Transfer experiments with Neotropical Littorinidae showed radular changes within 40 days (Andrade & Solferini, 2006). In freshwater taxa, differences in radular morphology, distinguished by the shape and relative size of the denticulation, are present both within species flocks in ancient lakes (Rintelen et al., 2004) and between partly isolated populations (Hunter, 1975; Evans, 1989). Even food deprivation events lead to modifications in radular secretion after 120 days (Smith & Russel-Hunter, 1990). Such differences can be attributed to ecophenotypic plasticity, which does not support hypotheses of geographic race formation or incipient speciation (Hunter, 1975; Evans, 1989; Smith & Russel-Hunter, 1990; Andrade & Solferini, 2006).



FIGS. 57, 58. Histology of male pallial gonoduct of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 120871). FIG. 57: Cross section of prostate at level of spermatophore forming organ (see Fig. 50); FIG. 58: Detail of spermatophore forming organ (arrow indicates sperm). Scale bars = 0.25 μ m.

Similarly, significant variation in fecundity within species has been found between populations of tropical viviparid snails determined by such factors as periphyton quantity and quality, population density, current velocity, and physio-chemical variables, including water temperature, dissolved oxygen, and calcium concentrations (New South Wales, Department of Primary Industries, 2007). For other freshwater snails, Dillon (2000) also established that higher current velocities (as caused by rainfall) could be responsible for lower survivorship and fecundity. Searching for environmental factors that could correlate with brood differences between Jamaican populations, it was found that specimens from Anchovy-Gully were sampled during the dry season (July), whereas the Black River specimens were collected during the peak of the rainy season (October). Further sampling will be necessary to establish if the observed differences are a consequence of seasonality.

Consequently, the above-mentioned differences between populations are interpreted as representing intraspecific variation. It can be concluded that *Hemisinus* is represented in Jamaica by only one native species.

Reproductive Biology

Based on the fact that thiarids are generally referred to being parthenogenetic, Nuttall (1990) reported this condition for *Hemisinus*. However, similar proportions of males and females were found in this study, indicating that sexual reproduction is likely the reproductive mode in Jamaican *Hemisinus*.

According to Strong et al. (in press), both Bayesian and parsimony analyses support Paludomidae and Thiaridae as sister taxa based on molecular and combined molecular/morphological data but not on morphological data alone, which could be product of the lack of information for *Hemisinus*. Consequently, information on *Hemisinus lineolatus* morphology is compared to that of other members of the Thiaridae and Paludomidae (Table 4). Some of the more significant findings of this study relate to new insights into reproductive biology. The male pallial gonoduct in *H. lineolatus* is almost completely open, as in other Thiaridae (Starmühlner, 1969; Muley, 1977). In paludomids, however, the male gonoduct is mostly closed and forms a tubular, anterodorsal spermatophore organ, which typically opens to the anterior third to half of the gonoductal groove. A similar structure, also dorsal but positioned more posteriorly along the axis of the gonoductal groove, is present in *H. lineolatus* (Figs. 50–52). Based on a similar basophilic epithelium to the organ of paludomids, and the presence of sperm (Figs. 57, 58), it is inferred to be a spermatophore-forming organ. However, no spermatophores were found in *Hemisinus*. If homologous in the two families, the structure has been lost by most other members of the Thiaridae, and has become more prominent (i.e., visible externally) and shifted anteriorly in the Paludomidae.

Most thiarids are characterized by an unusual pallial oviduct that is a bilaterally symmetrical, non-glandular tube, with a large, medially placed bursa (Starmühlner, 1969; Schutt & Glaubrecht, 1999; Strong et al., in press). The

TABLE 4. Summary of morphological differences between *Hemisinus lineolatus* compared to other limnic gastropods in the Thiaridae (*Thiara*) and Paludomidae (*Vinundu*, *Lavigeria*, *Tiphobia*). Data from Starmühlner, 1969; Schütt & Glaubrecht, 1999; Strong & Glaubrecht, 2002, 2003, 2007, 2010; Michel, 2004; Ben-Ami & Hodgson, 2005. Abbreviations: ct, ctenidium.

	Thiaridae		Paludomidae		
	<i>Hemisinus</i>	<i>Thiara</i>	<i>Vinundu</i>	<i>Lavigeria</i>	<i>Tiphobia</i>
Shell					
Juvenile shell	Smooth	Smooth	Granulose	Wrinkled	Wrinkled
External Anatomy					
Operculum	Paucispiral	Paucispiral	Paucispiral	Paucispiral	Concentric, Paucispiral nucleus
Operculum nucleus	Eccentric	Eccentric	Subcentral to eccentric	Subcentral	Subcentral
Mantle edge	Papillate	Papillate	Lobate	Lobate	Smooth
Osphradium length	1/3 ct	~1/2 ct	3/4 ct	~1/2 ct	~1/3 ct
Alimentary System					
Rachidian	Pentagonal/Broad	Short/Broad	Rectangular	Rectangular	Rectangular
Rachidian basal denticles	Present	Present	Absent	Absent	Absent
Rachidian denticles	2–3/1/2–3	3–6/1/3–5	2/1/2	1/1/1	8–15/1/8–15
Lateral denticles	2–3/1/2–3	2–6/1/2–5	2/1/2	1/1/1	3–6/1/5–16
Marginal denticles	4–5	6–8	5–10	1–5	5–8
Accessory pad	Large, Textured	Large, Textured	Small	Small	Small
Caecal folds	2	2	Absent	1	1
Caecum	Shallow	Deep and spiral	Shallow?	Shallow	Shallow
Style sac typhlosoles	Fused	Fused	?	Partially fused	Partially fused
Reproductive System					
Renal oviduct	Branched	Branched	Unbranched	Unbranched	Unbranched
Pallial oviduct	Glandular	Non–glandular	Glandular	Glandular	Glandular
Spermatophore bursa placement	Lateral lamina	Medial	Medial lamina	Medial lamina	Medial lamina
Spermatophore organ	Mid–dorsal	Absent	?	Anterior	Anterior
Nervous System					
Statocyst	Statoconia	Statolith	?	Statoconia	Statoconia
Right dialyneury/zygoneury	Dialyneury	Dialyneury	Zygoneury	Zygoneury	Dialyneury

renal oviduct is bifurcate, sending one branch to enter above the bursa, and another to open far anteriorly above the vagina. *Hemisinus* differs from this pattern in possessing a pallial oviduct that is glandular and distinctly asymmetrical,

with an albumen gland elaborated posteriorly, and with a large bursa in the lateral lamina. However, the typical thiarid branching pattern of the renal oviduct is retained. The conditions present in *Hemisinus* indicate that the unusual

“thiarid” bursa is derived from a sperm storage pouch located within the lateral lamina. The homology to sperm storage pouches in this location in other taxa remains unknown; no sperm storage pouches in the lateral lamina are known in paludomids.

In thiarids, brooding is a common life history trait and is known in all species of the family except *Pachymelania* (Glaubrecht, 1996). Here, the eggs complete their development within a cephalic brood pouch and the young hatch as swimming veligers or crawling juveniles (Muley, 1977). The brood pouch overlies the esophagus in the dorsal cephalic hemocoel, and extends back from a brood pore on the neck. The brood pouch of *H. lineolatus* has the same arrangement but differs from some members of the family (i.e., *Tarebia granifera*, *Thiara scabra*, *T. amarula* and *M. tuberculata*) in its internal structure and in the embryonic developmental stages that are present. Typically, the brood pouch has separate individual compartments formed by columnar epithelium that extends into the brood pouch cavity (Strong & Glaubrecht, 2007; Table 2). Such compartments may be occupied by several early embryonic stages or thousands of developing larvae. In *H. lineolatus*, despite that these kinds of cells are also observed, they do not form compartments and there is no evidence of any early stages inside the pouch.

In thiarids, it has been assumed that energy for embryonic development in the brood pouch may be derived from storage products in the eggs, from the mother or from adelphophagy (Hodgson et al., 2002). Lecithotrophic nourishment of the embryos in freshwater thiarids is known for *Fijidoma*, *Melanoides*, *Tarebia* and the South American *Aylacostoma* (Strong & Glaubrecht, 2007). Embryonic nourishment in *H. lineolatus* is still unknown.

Affinities of *Hemisinus lineolatus*

Morrison (1951), based on operculum and external head-foot features, included *Hemisinus* within the Thiaridae, a view that has not been changed since. Comparison of *Hemisinus lineolatus* with thiarids and paludomids (Table 4), shows that *Hemisinus* exhibits many typical thiarid characteristics, such as the structure of the operculum, mantle edge, rachidian (shape, basal denticles), midgut (large, textured accessory pad; two short, prominent caecal folds; fused typhlosoles), renal oviduct (branching), and cephalic brood pouch. It also shares some anatomical similarities with paludomids (stato-

conia, spermatophore organ), especially basal paludomids (mantle papillae, right dialyneury) (Strong, unpubl. data). Some of the anatomical differences between *Hemisinus* and other thiarids (e.g., glandular pallial oviduct with bursa in lateral lamina) could indicate that it does not group within the Thiaridae. However, it is more parsimonious to conclude that the features shared with paludomids, in combination with its unique anatomical attributes, are consistent with a basal position within the Thiaridae, a position thus far supported in phylogenetic analyses of the superfamily, albeit with limited taxonomic sampling and incomplete anatomical information (Lydeard et al., 2002; Strong et al., in press).

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